Trends in adult coho and chinook salmon life history at the University of Washington's hatchery

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November 2000

Abstract

The declines in abundance of Pacific salmon in the northwest have greatly increased the need to fully understand the status and trends of species and populations in the region and especially Puget Sound over the past several decades. To advance our state of understanding, we examined detailed data on the University of Washington hatchery populations of coho and chinook salmon, recorded since the late 1950s. Specifically, we assessed trends in timing of spawning, body size (length and weight) and reproductive traits (fecundity and egg size). The date of spawning for both species (but particularly coho salmon) occurred earlier over the years but seems to have stabilized in recent years. Salmon of both species have declined in average length and weight over the entire period of record but since the late1970s both species (especially coho) have also gotten thinner (i.e., lighter for a standard length). The patterns of fecundity at a standard length parallel those of weight; fecundity at length increased until about 1980 and decreased thereafter. An opposite pattern was observed in egg size; lately salmon (especially coho) are relatively small but are producing large eggs for their body size and consequently far fewer eggs than in the past (over 3000 per female around 1970 to under 2000 lately). Condition factor, and fecundity of both species showed declines over the past several decades, notably since the late 1970s or about 1980. The incidence of jacks has varied considerably from year to year but two age groups of jacks are seen in chinook. Age-2 jacks were most abundant until the late 1970s, when they decreased and age-1 jacks became more common. Overall, the results point to some trends, notably timing, that are probably related to practices in the hatchery and other trends, notably size and reproductive traits, that may reflect a mix of condition of the salmon when released and the environmental conditions that they experienced at sea. Further analysis will be directed at disentangling these factors.

Introduction

The declines in abundance of Pacific salmon in the northwest and the application of the United States Endangered Species Act to evolutionarily significant units (ESUs) within species have greatly increased the need to fully understand the status and trends of species and populations in the region over the past decades. It is generally acknowledged that there were periods in the century when salmon were scarce in Alaska, relative to present levels, and at the same time populations in the Pacific Northwest were comparatively abundant. This "regime" seems to have shifted in the late 1970s and since that time there have been relatively weaker runs in the Pacific Northwest and stronger runs in Alaska and northern British Columbia (Francis and Sibley 1991; Beamish and Bouillon 1993; Francis and Hare 1994; Hare et al. 1999).

In addition to changes in abundance, there have also been changes in body size documented in many salmon populations, and most have shown declines (Ricker 1980; Helle and Hoffman 1995, 1998; Bigler et al. 1996). Changes in size at maturity or growth rate at sea seem to be affected by both density (i.e., competition: Rogers and Ruggerone 1993; McKinnell 1995) and environmental conditions, notably temperature or some correlate of it (Pyper and Peterman 1999). Abundance appears to have a much greater effect on body size than temperature, at least some species that feed in the open ocean such as sockeye (Pyper and Peterman 1999). However, despite their low abundance, Pacific Northwest (e.g., Washington and Oregon) stocks of some species are also experiencing decreases in body size (coho salmon: Weitkamp et al. 1995). There are many possible explanations for changes in body size (Ricker 1980), including selective effects of fishing, loss of large-bodied populations, environmental change (i.e., growing conditions at sea) and propaga-tion in hatcheries. Such reductions in size may be accompanied by reductions in fecundity (which would obviously affect productivity), egg size (which might affect the survival of offspring after emergence) and egg burial depth (Beacham and Murray 1993; Steen and Quinn 1999).

The environmental influences on growth (food, competition and temperature) are obvious but growth is also under some degree of genetic control. There is variation in growth among strains or families under controlled conditions (e.g., rainbow trout, *O. mykiss* Richardson: Iwamoto et al. 1986; Wangila and Dick 1996; chinook salmon: Withler et al. 1987; Heath et al. 1993; brook trout, *Salvelinus fontinalis* Mitchill: Ferguson et al. 1995; Atlantic salmon, *Salmo salar* L.: Jonasson 1993; pink salmon: Smoker et al. 1994; chinook salmon: Unwin et al. in press). Breeding programs have also demonstrated a response to selection for growth (e.g., chinook salmon: Donaldson and Menasveta 1961; coho salmon, *O. kisutch* Walbaum: Hershberger et al. 1990). Growth rate and smolt size are linked to maturation (Brannon et al. 1982) but there are population-specific patterns in age at maturity (e.g., Roni and Quinn 1995), again under some measure of genetic control (e.g., Hard et al. 1985; Hankin et al. 1993). The population-specific variation in size and age at maturity can apparently evolve quite quickly (Quinn and Unwin 1993).

A balance between environmental and genetic factors affects the timing of return migration by salmon as well as their growth and age at maturity. The timing of return is affected by conditions at sea (Blackbourn 1987) and in rivers (Quinn and Adams 1996) but in general there is a large measure of genetic control over the time of migration and reproduction in salmonids (Siitonen and Gall 1989; Hansen and Jonsson 1991; Su et al. 1997; Smoker et al. 1998; Quinn et al. 2000).

The balance between environmental

and genetic control over life history traits is not limited to growth, age at maturation and timing of migration and maturation. The size and number of eggs produced by females is also under complex controls. In general, large females produce more eggs and larger eggs than smaller females, though there is considerable variation among populations (Beacham and Murray 1993; Quinn et al. 1995). Within and among populations, variation has a genetic basis (Bromage et al. 1982; Su et al. 1997; Kinnison 1999). However, within populations, females that grow rapidly early in life tend to have more eggs (and consequently smaller eggs), for given length than females that grew slower (Thorpe et al. 1984; Jonsson et al. 1996). Thus, juvenile growth rate can influence offspring quality and quantity.

Thus there are complex combinations of environmental and genetic factors affecting not only survival but a series of key life history traits in salmonids: growth, age at maturity, timing of migration and reproduction, and egg size and fecundity. All of these traits can be affected, directly or indirectly, by artificial propagation of salmonids in hatcheries. Growth rates are accelerated compared to those in most wild populations, by slightly increasing the water temperature and feeding large quantities of nutritious food. Size of juveniles may affect survival at sea and also the tendency to mature (larger fish or faster growing fish generally mature where smaller or slower growing fish remain at sea for another year). The hatchery can affect timing of maturation if they spawn all the early arriving fish and discard late fish if the capacity of the hatchery has been exceeded, or by differential survival of progeny of early and late fish. One might predict an evolutionary trend towards high fecundity and small eggs in hatchery populations over time so that females could maximize their reproductive success. Size-selective predation, common in natural systems, is eliminated in hatcheries and off-

spring from small eggs quickly catch up to those from larger eggs in size (Kinnison et al. 1998; Heath et al. 1999). The purpose of this study is to investigate (1) any changes in time of spawning, (2) change in body size over time, (3) change in reproductive output (egg size and fecundity), and (4) the increased incidence of precocious maturity in the populations of coho and chinook salmon in the University of Washington's hatchery since the 1950s to provide insights into the ecology of Puget Sound salmon.

Background

In the early 1930s, while a graduate student, the late Lauren Donaldson conducted experiments on the growth and culture of salmon and trout at the UW campus. However, it was not until after the Second World War and his subsequent research on radiation ecology that Donaldson conceived and constructed a salmon and trout hatchery on the UW campus, and the first chinook salmon were released in 1949. It was modified somewhat when a bulkhead was built, turning a cove in Portage Bay into a holding pond for adults in 1960, but has otherwise been structurally similar over much of its existence. Coho (and sockeye) experiments in the early years were not very successful but starting in the late 1960s there were substantial numbers of coho salmon returning, along with the chinook. The stocks of chinook and coho salmon Dr. Donaldson used were primarily from the Green River system (Soos Creek hatchery), though some exchange with other populations took place over the years. Since the early days of the hatchery (late 1950s), all returning salmon were identified, measured for length, and weighed, and the date was recorded, along with any marks or unusual circumstances. For a large number of the females, fecundity and egg size were also measured. This represents a priceless and

unique record of salmon spawning date, size, and reproductive output in the Lake Washington basin. The detail of these records far exceeds that available for other hatchery or wild populations.

Analysis and interpretation of such data, collected in the past, must be done cautiously. There has been a great deal of publicity regarding Dr. Donaldson's selective breeding of rainbow trout, but the chinook salmon were also subject to selection, especially in the early years (1953-1972). The objectives of the selective breeding program were to develop chinook salmon with the same qualities of strength, growth, and fecundity as the rainbow trout (Hines 1976). This included maturing at an early age, produce maximum accelerated growth, have an increase in fecundity, and have a high survival rate of eggs, fry, and fingerlings. Then there were the objectives more specific to salmon, such as, accelerate the rate of growth to reduce the time to migration, have an increase in adult survival at sea, shorten the spawning cycle, and spawn at a specific season (Donaldson and Menesveta 1961). The methods used to accomplish the objectives of the selective breeding program were: (1) select three year olds to breed to try and shorten the spawning cycle from 4 years to only 3 years, (2) select females by best weight, color, and productivity, (3) select the very finest males by weight, color, and ability to fertilize many females eggs, (4) select eggs from females that produce eggs with high rates of survival, and (5) make selections at the fry and fingerling stages to eliminate fish showing evidence of disease, poor growth (development not at optimum rate), and high incidence of malformation (Hines 1976). The selective breeding is described in more detail in Donaldson's reports (e.g., Donaldson and Menasveta 1961; Donaldson 1970) and the book about his work by Hines (1976). Some degree of selection is common and perhaps inevitable in hatcheries, and it is unclear how much the phenotype of the population was affected by these efforts.

Methods and Materials
Data Collection
Spawning Methods

Over the years at the University of Washington hatchery the process of harvesting the salmon occasionally occurred daily but typically three times each week, on Monday, Wednesday and Friday. On each day of spawning, the water level in the pond was lowered, dead fish were removed and set aside for later measurements. A seine net was used to gradually encircle every fish, and move them to one area of the pond near the shore where all the sample and data collection equipment was located.

Each fish was handled and identified to species and sex, and checked for ripeness to spawn. If the fish was ripe it was sacrificed and given a numbered paper tag that stayed with it throughout the entire data collection process. Any fin clips, marks, brands or tags were recorded, weights were taken to the nearest 0.01 kg, and fork length was measured to the nearest mm. If coded wire tags were detected, the snout was removed, the tag removed and read, and the data recorded. This was helpful in determining the ages of fish, especially since no otoliths or scales were taken prior to 1999. The females were then stripped of their eggs into sanitized buckets where the milt from the males was squeezed from their bodies over the eggs and mixed. While evenly distributing the milt over the eggs, the eggs were checked for water hardness and immaturity (green). If the percentage of bad eggs was high the egg lot was thrown out, and if females were noticeably immature they were not used. Then the buckets with the eggs and milt were taken into the hatchery to activate the fertilization process by adding water and Wescodyne for disease control. The eggs were then placed into vertical-stack

Heath tray incubators; typically the eggs from each female were in a separate tray so they could be tracked by the spawning number corresponding to the male and female parents.

Incubation and Rearing Methods

The UW hatchery's main water source is the Lake Washington Ship Canal, which drains the epilimnion of Lake Washington. Consequently, it is too warm in the summer to rear Pacific salmon. To accommodate this feature of the site, the coho salmon are reared on an accelerated regime of temperature and food to reach a suitable size for smolt transformation in their first spring of life. The chinook salmon are ocean-type (i.e., underyearling migrants) as is characteristic of lowland Puget Sound stocks including the primary donor stock, the Green River. They therefore are also released as smolts in their first spring. The hatchery incubates embryos in warmer water ($13\text{-}16^0$C) than salmon would ordinarily experience, causing them to hatch and complete yolk absorption early in winter so the fish attain a greater size before release.

Dead eggs are removed 24 hours after fertilization. When the embryos reach the eyed stage they are shocked (dropped from an elevated position into a container to eliminate those that were not developing normally), counted and measured. Dead eggs are removed by hand with modified metal tongs, counted and entered as data to be added to the estimated fecundity. The number of eggs produced by each female are determined by recording the volume of water displaced by the eyed embryos (Allen 1958) and their average volume, estimated from average egg diameter. Egg diameter is determined by counting the number of eggs that fill a 6" trough. To convert these volumetric estimates of egg size at the eyed stage to weights of fresh (unspawned eggs), we collected data in 1992 (chinook salmon only) and 1999 (coho and chinook salmon). A subsample of fresh eggs (circa 50-

100 eggs) were weighed and counted, and the entire egg mass was weighed. Fecundity, estimated arithmetically from these gravimetric data and mean egg weight, was then compared to volumetric fecundity estimates and diameters of eyed eggs measured in the traditional manner on the same females.

Once the alevins hatched and absorbed their yolk sac they were moved from the incubators into concrete raceways for feeding. As they became crowded in the small raceways inside the hatchery facility they were moved into the larger raceways outside. The coho and chinook offspring from the egg stage to the fingerling stage were kept separated by species until March when they were moved into a large earthen pond together where they were fed until time of release in May. At the time of release, the pond screens are removed from the outlet that leads to Portage Bay and feeding is terminated. Within a week if fish are still in the pond the water flow to the pond is stopped, forcing them to leave. Migration into salt water is volitional since the productivity of the Washington Lake system is adequate enough to allow extended rearing in the fresh water if fish are not ready to migrate to sea (Brannon et al. 1982).

Data Analysis

Data were collected from hand-written records that were stored in books and folders at the University of Washington hatchery from 1953 through the late 1980s, and data that had already been entered digitally from the late 1980s through early 1990s. All the data were entered into the Spreadsheet program, Microsoft Excel, and then later into Microsoft Access. The data used for this study included species (only coho and chinook salmon data were examined), number associated with each fish, date when it was spawned, sex, marks (codes), length, weight, egg lot number, number of eggs per trough, fecundity, whether the fish died in the pond or was killed for

spawning, and any comments connected with the fish. Data created from the original records through formulas, conversions or ancillary data included observed age, estimated age, average egg diameter and egg weight, total mass of eggs, and the gonadosomadic index (% of total body weight in egg mass).

Change in body size over time

Our goal was to test the null hypothesis (that body size has remained the same) against the predicted alternative hypothesis (body size is declining). Salmon were excluded from the length analysis if their body length was compromised or estimated because of several factors (e.g., decomposed, mutilated, head or snout missing). Salmon were excluded from the weight, and condition factor (length to weight relationship) analyses if their body weight was compromised (e.g., partially or completely spawned-out when weighed, died in the pond, mutilated, scavenged, body parts missing, etc.).

In addition to looking at overall size trends, we have tried to look at size at a given age. The estimation of age for each fish to obtain mean lengths at a given age was performed by a combination of two methods: analysis of marked fish and length-frequency histograms. Some fish were marked as smolts with a variety of techniques, including fin clips, brands and coded wire tags. These marks were used to determine the ages of returning chinook and coho salmon from those release groups. Scale and otolith samples have not been taken until 1999 so unmarked fish were of uncertain age. Such salmon, and those with marks that were not unique to one brood year, were aged by length-frequency distributions that showed the age composition as separate modes, assessed visually. This method is most accurate for younger fish (e.g., age 1 vs. 2). For example, coho were separated readily into age classes 1 and 2 but we had to assume that there were no fish of age 3 in the population

based on the general biology of the species. Chinook were separated into age groups 1, 2, and 3+, but the latter category includes fish aged 4 and perhaps a very few aged 5. Length frequency distributions [LFD] for adult male and female chinook and coho salmon have been plotted as histograms for each year over the periods of 1957-1999. In addition to looking at trends in length and weight separately, we are also examining the allometric relationship between length and weight. We characterized the relationship by regressing mean weight against mean length of annual returns to estimate the two parameters, a and b. This will allow us to determine if the fish are lighter for a given length than in the past, using the relationship:

$$M = a(FL)^b$$

Transformed to $LogM = Log\ a + bLog(FL)$, where M is the measurement (weight) and FL is the fork length (Ihssen et al. 1981). An adjusted value was calculated for each fish in each year, and then annual means and adjusted mean weights were calculated.

Fecundity and egg size

We are interested in the trends of reproductive output (egg size and fecundity) for female salmon over the years. Fecundity and egg size have been measured for a large proportion of the individual females in a standard manner over the years. The average fecundity over the years was calculated and plotted for chinook and coho. We also looked at the relationship between egg size and fecundity for both species, and average fecundity and egg size for a given spawner size, to determine if the patterns of reproductive allocation have changed over the years with changes in body size. This was accomplished by standardizing fecundity, egg size, and total fish weight to the overall mean fork length of all adult salmon for all years by species (stan-

dard coho salmon length = 545 mm; chinook = 785 mm). This method followed Ihssen et al. (1981):

$$M_{adj} = M_o \times (L'/L_o)^b$$

Where M_{adj} is the adjusted character, M_o is the observed character, L' is the grand sample mean fork length of all females over all years, L_o is the observed fork length, and b is the regression coefficient (slope) of $LogM_{adj}$ on $LogL_o$ within populations.

Spawning Date

Based on anecdotal reports, we hypothesized that chinook salmon are tending to spawn later and coho salmon earlier than in the past. Only female spawners were used to determine the timing of spawning since females were taken and spawned when they were fully ripe, thus ready to spawn. The males, even when ripe could actually stay alive for a longer period of time than females, so sometimes they were held on to until ready to use, sometimes up to a week or more. Almost all jacks and some older males were killed but not spawned so their date of sampling bears little relationship to date of maturity. Females that were already spawned-out (spent) or partially spent were used for the analyses, since the actual spawning date would have only been no more than a day or two from the observed date. Females that were spawned but were not fully mature when killed were excluded from the analysis, as were females that died in the pond. The mean and median spawning dates for each year and species were calculated but the median was used for analysis because it expressed central tendency (Zar 1996) more adequately with skewed populations than the mean for our purposes. That is, the median was not affected as much as the mean by occasional females that were spawned extremely early or late.

Precocious Maturity

We examined the incidence of precocious maturity in both the coho and chinook salmon. Some coho males return as "jacks" after one summer at sea and are much smaller than the older males and females. The chinook show two age groups of jacks: those maturing after one full year at sea and a summer (i.e., age 2) and "mini-jacks" that return after only a summer at sea (as with the coho jacks). Females are not represented in either of these two age groups. The analysis of the precocious males included all fish that returned at the size indicating that thefish was a jack (length-frequency analysis) or if the age was known as a 1 or 2 year old for chinook and a 1 year old for coho. Since we were interested in the incidence and size of jacks and mini-jacks, all such fish were included in the analysis, even if they died in the pond. However, there may be a slight under-estimate of the number of coho salmon jacks and chinook mini-jacks because of predation in the pond from blue herons.

Size at Release of Juveniles

The release statistics are less robust than those of the returning adults because individual fish are not measured. Instead, fish are weighed in bulk and counted to produce an overall average weight per fish but no variance per individual fish. We examined the interactions between release size and date, and associated patterns in returning adults (e.g., age and size at return). The smolt release data were combined with the adult salmon returns by attaching the smolt group information that matched the adult fish in that group by the type of fin clips, marks (brands), or codes (coded nose wire tags). There are several dimensions to this activity since a variety of treatments have been applied. For example some released fish over the decades were treated with special temperature regimes, irradiation, nutritional adjustments and age-specific breeding schemes. Our analysis at this

point includes all releases except those that occurred early in the year (pre-smolt releases, defined as earlier than March) or in locations other than the UW hatchery.

Results

Coho Salmon

Spawning date

Coho salmon are spawning earlier at present than in the past, as indicated by the median date (slope = -0.57, r2 = 0.28, Figure 1). The variation in spawning date, indicated by the standard deviations of the mean spawning date, also showed a reduction in days. Thus the spawning season has become earlier and shorter (Table 1). In the first 20 years the peak of the spawning season ranged from late November to mid-December and in the most recent 25 years the peak of the spawning season has occurred from early November to mid- to late November.

Body size

Coho body size in adult males and females has declined in length and weight over time. Annual average length of females had a maximum difference of 193 mm: from 661 mm in 1965 to 468 mm in 1997. Annual average weight of females had a maximum difference of 2.31 kg: from 3.52 kg in 1973 1.21 kg in 1992. There are two age groups of males (age-1 and age-2). The declines in length and weight were dramatically seen in
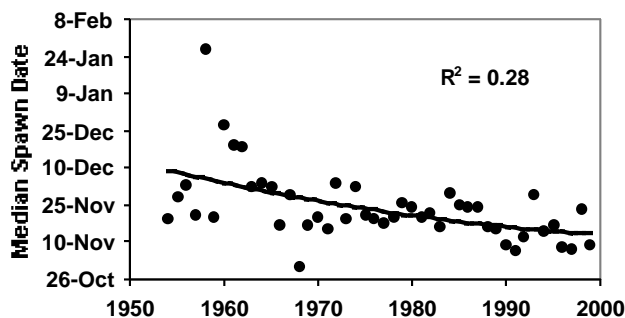

Figure 1. *Median spawn date of female coho salmon that returned to the University of Washington pond from 1954-1999.*
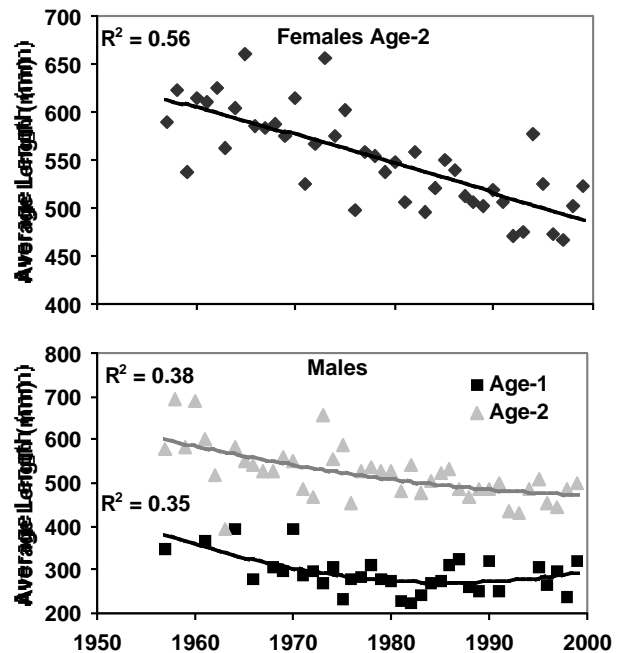

Figure 2. *Average length at age of female and male coho salmon that returned to the University of Washington (UW) ponds from 1957-1999.*

the age-2 males, and the age-1 males, or jacks, experienced a slight decrease in length and weight until the 1980's (Figure 2). The highest average length for male coho at age-2 was in 1973 at 658 mm while the lowest was in 1993 at 431 mm, a difference of 227 mm. Then the highest average weight for age-2 male coho was at 2.51 kg in 1975 and the lowest was 0.86 kg in 1992, a difference of 1.65 kg. Some 3 year olds, male and female coho have returned to the UW hatchery, as revealed in the years when the fish were marked but they have been so scarce (<1%) that they were not analyzed separately but combined with the age-2 fish.

Since, the average length and weight over time for both sexes has been declining we looked to see if they appeared to be correlated with each other. The male and female average lengths and weights over time did appear to be correlated with each other, when length decreased weight also decreased and vice versa (Figure 3). We also looked at the condition

Table 1. Summary of the female coho salmon median and mean spawn dates, and standard deviation (Stdev) of days for each year from 1954-1999. The sample size (N) was the number of females used to obtain the spawning dates and standard deviations.

| Year	N	Median Date	Mean Date	StDev
1954	69	19-Nov	21-Nov	13
1955	17	28-Nov	25-Nov	23
1956	47	3-Dec	27-Nov	23
1957	48	21-Nov	27-Nov	15
1958	10	27-Jan	22-Jan	6
1959	9	20-Nov	19-Nov	5
1960	10	27-Dec	14-Dec	17
1961	43	19-Dec	22-Dec	19
1962	38	18-Dec	11-Dec	8
1963	22	2-Dec	13-Dec	18
1964	112	4-Dec	6-Dec	15
1965	8	2-Dec	28-Nov	6
1966	33	17-Nov	10-Nov	20
1967	10	29-Nov	17-Nov	24
1968	26	31-Oct	2-Nov	22
1969	74	17-Nov	19-Nov	29
1970	34	20-Nov	30-Nov	20
1971	67	15-Nov	18-Nov	24
1972	482	4-Dec	1-Dec	17
1973	1616	19-Nov	21-Nov	10
1974	795	2-Dec	3-Dec	12
1975	827	21-Nov	16-Nov	18
1976	200	19-Nov	26-Nov	33
1977	586	18-Nov	22-Nov	12
1978	249	20-Nov	23-Nov	11
1979	519	26-Nov	27-Nov	12
1980	519	24-Nov	25-Nov	12
1981	1063	20-Nov	20-Nov	11
1982	424	22-Nov	17-Nov	16
1983	612	16-Nov	18-Nov	17
1984	1038	30-Nov	29-Nov	10
1985	945	25-Nov	24-Nov	13
1986	1198	24-Nov	23-Nov	13
1987	530	24-Nov	23-Nov	15
1988	104	16-Nov	16-Nov	17
1989	244	15-Nov	17-Nov	8
1990	88	9-Nov	11-Nov	7
1991	67	6-Nov	10-Nov	10
1992	191	12-Nov	19-Nov	12
1993	67	29-Nov	1-Dec	14
1994	32	14-Nov	15-Nov	13
1995	294	17-Nov	16-Nov	11
1996	248	8-Nov	15-Nov	1
1997	290	7-Nov	14-Nov	11
1998	339	23-Nov	24-Nov	8
1999	267	9-Nov	9-Nov	8
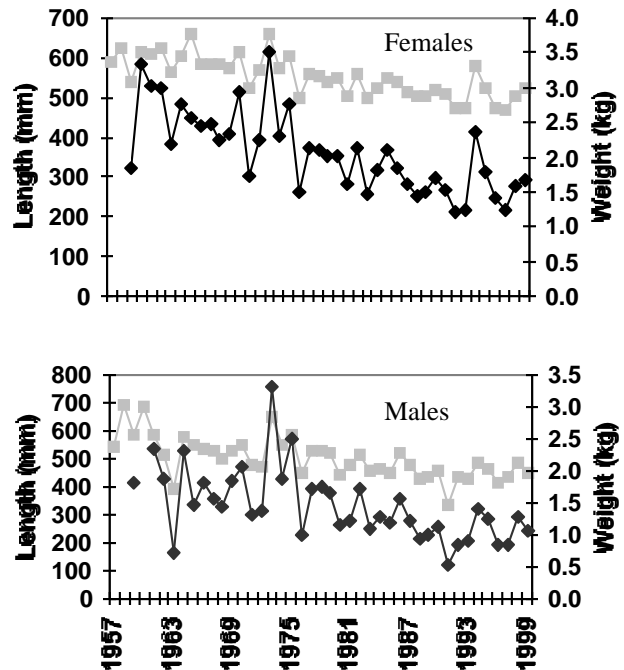
Figure 3. *Mean length (gray squares) and weight (black diamonds) of female and male coho salmon over time (1957-1999) that returned to the UW pond.*

factor (weight at a standard length) of all the coho salmon combined (male and female). In the early years (1957-1970's) the condition factor of the fish was high but declined through the 1980's and 1990's (Figure 4). In 1973 the condition factor was at its highest (length 655 mm, weight 3.42 kg), and the lowest annual average was in 1991 (length 380 mm, weight 0.75 kg). Thus the coho salmon have been getting progressively shorter and also thinner.

Fecundity and egg size

The analysis of the raw values for fecundity and egg size (diameter) of coho salmon revealed declines in both characteristics (Figure 5), as expected given the reduction in length and weight over time. For example, in 1973 the average length of female coho was 657 mm, weight was at 3.52 kg, and fecundity was 3799 eggs, whereas in 1993 the average length was 475 mm, weight was 1.25 kg, and fecundity was 1351 eggs, a difference of 222
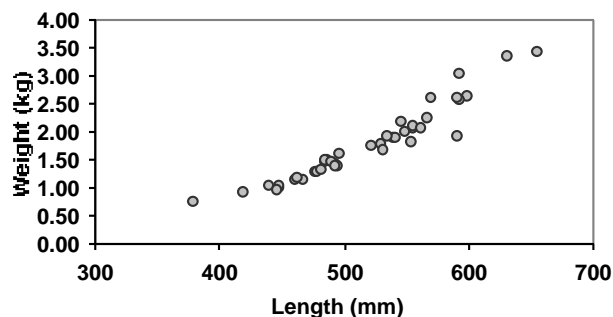
Figure 4. *Condition factor (allometric relationship) of all male and female coho salmon combined. Each circle represents an entire year, which ranges from 1957 to 1999.*
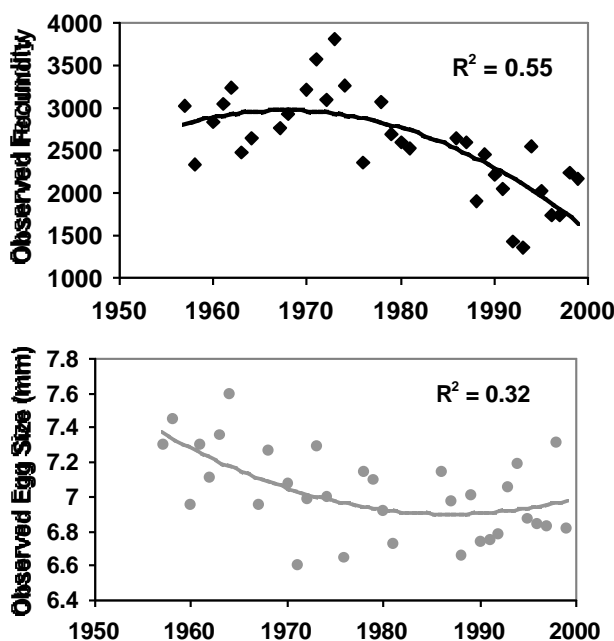

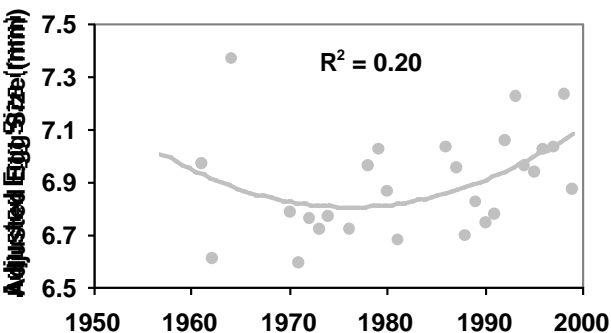Figure 5. *Observed fecundity (black diamonds) and egg size (gray circles) of female coho salmon at UW hatchery from 1957-1999.*

Figure 6. *Female coho weight (graph1), fecundity (graph 2), and egg size (graph 3) adjusted to a standardized length of 545mm from 1957-1999.*

mm, 2.27 kg, and 2448 eggs. After adjustment to a standard length of 545 mm, fecundity still showed a decline. For example, in 1978 the adjusted fecundity was 2949 eggs whereas in 1992 it was only 1771 eggs, a difference of 1178 eggs. It appears that in the earlier years (1957 -1970), weight and fecundity were low, increased during the 1970s but declined over the past 15-20 years. In contrast to fecundity, average egg size at a standard length has been increasing recently (Figure 6), and egg size and fecundity seem to show opposite trends.
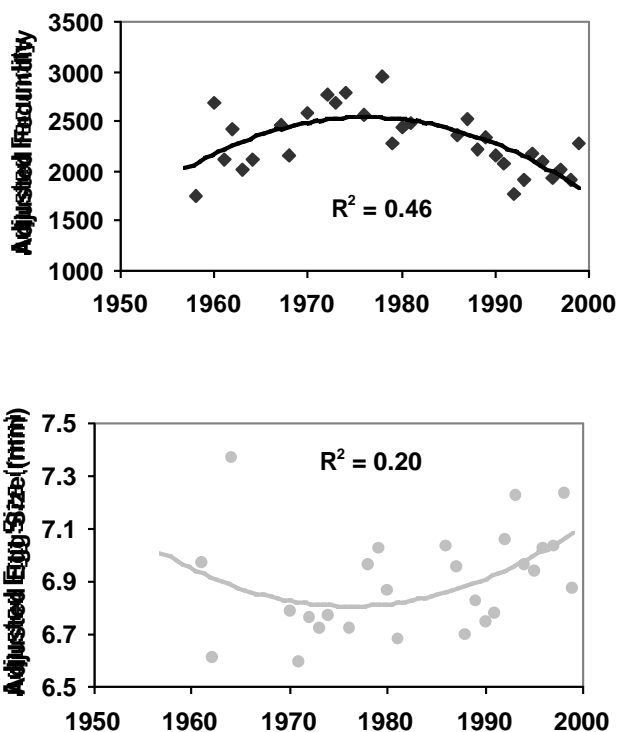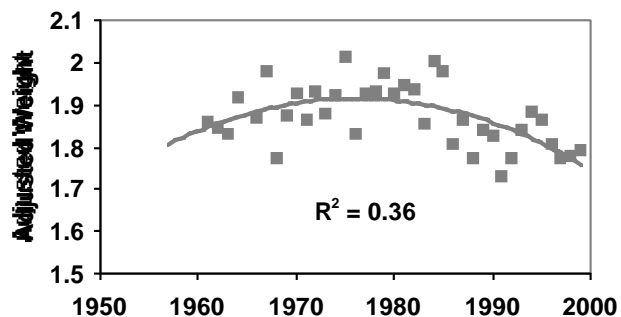
Precocious Maturity

The incidence of precocious maturity in male coho salmon ("jacks") has increased over the years at the UW hatchery (Figure 7). The coho jacks are only one year old, having spent only a summer at sea after release. They have been recorded since the first few years of the hatchery operation but were scarce. 1980 marked the first year where the proportion of jack returns to total male returns that returned to the ponds at UW hatchery was considerably

high (34%), and the incidence, reaching an all time high of 67% in 1991. The proportion of jack returns to the total male returns has been for the most part on the order of 10-20%, but since 1980 the incidence of jack returns exceeding 20% of the total male returns has become a common occurrence [i.e., 1980 (34%), 1985 (30%), 1988-89 (21%), 1995 (24%), 1991 (67%), 1996 (22%), 1999 (28%)](Figure 8). The increasing proportions of jack returns seem to coincide with periods of greater decline in length, weight, and condition of the returning coho salmon.

Chinook Salmon

Spawning Date

Chinook salmon date of spawning has become earlier from 1954-1999 (slope = -0.19; r2 = 0.31), but the change has not been as large as in the coho salmon. The chinook median spawn date by year showed a slight decline
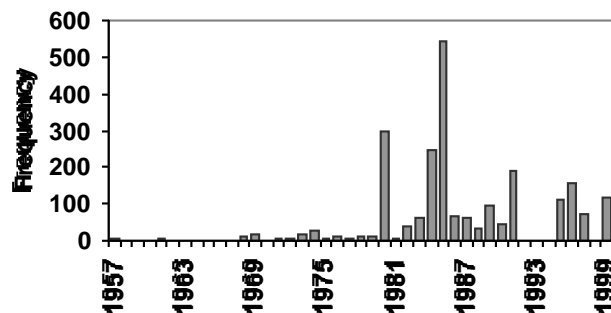
Figure 7. *Frequency of coho jacks returning to the UW hatchery from 1957-1999.*
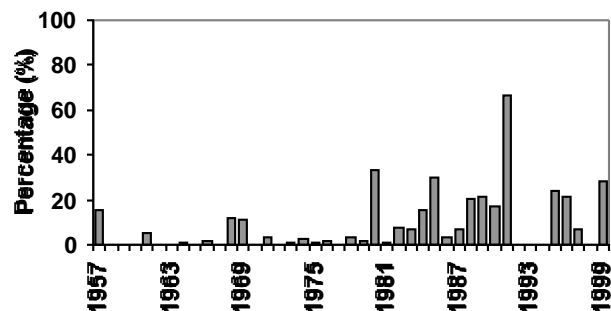
Figure 8. *Proportion of coho jack returns to the total male returns at the UW hatchery from 1957-1999.*

(earlier spawn time) over time (Figure 9). In the past (first 20 years) the peak of the spawning season ranged from late October to mid-November, and in the past 25 years the peak of the spawning season has been very consistently within the last week of October. The standard deviations of the mean spawning date showed a reduction in the spawning timing from the early 1960's to 1980 but since then it has increased (Table 2).

Body Size

Males and females (all ages combined) have been declining in length and weight over time (Figure 10). However, because of the many age classes that can be found in a chinook population, this decline could be caused by having a very large number of younger age classes returning, thus pulling down the average length and weight. This is probably not the case for females because they usually mature at age-3 (44%) and age-4 (56%). However, males mature as young as age-1 (micro-jacks) and age-2 (jacks)(Figure 15). Of the older male salmon, 77% are age-3 and 23% are age-4. Thus differences in size, the decline in length and weight, may be a function of the younger fish in the population.

Therefore, we looked at the change in length and weight over time by age classes to determine if the decline in size was a function of the diversity of age groups associated with size. The decline in size was shown in the
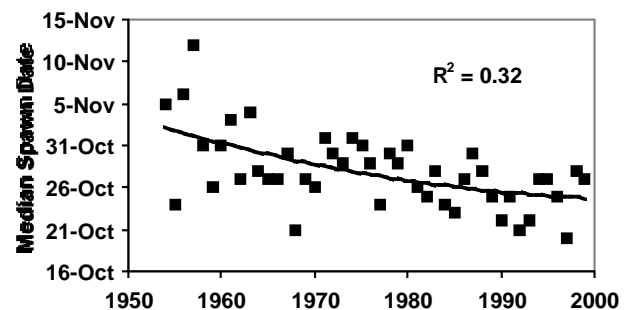
Figure 9. *Median spawn date of female chinook salmon that returned to the UW ponds from 1957-1999.*

Table 2. Summary of female chinook salmon median and mean spawn dates, and standard deviation (Stdev) of days for each year from 1954-1999. The sample size (N) was the number of females used to obtain the spawning dates and standard deviations.

| Year	N	Median Date	Mean Date	StDev
1954	8	5-Nov	10-Nov	12
1955	8	24-Oct	23-Oct	6
1956	28	6-Nov	6-Nov	11
1957	19	12-Nov	10-Nov	4
1958	354	31-Oct	1-Nov	8
1959	260	26-Oct	26-Oct	9
1960	102	31-Oct	31-Oct	8
1961	110	3-Nov	5-Nov	10
1962	163	27-Oct	27-Oct	9
1963	189	4-Nov	3-Nov	6
1964	205	28-Oct	27-Oct	8
1965	849	27-Oct	26-Oct	8
1966	714	27-Oct	28-Oct	7
1967	492	30-Oct	30-Oct	6
1968	932	21-Oct	23-Oct	8
1969	674	27-Oct	27-Oct	8
1970	1021	26-Oct	26-Oct	8
1971	515	1-Nov	3-Nov	6
1972	378	30-Oct	31-Oct	8
1973	498	29-Oct	29-Oct	7
1974	596	1-Nov	2-Nov	8
1975	927	31-Oct	31-Oct	7
1976	1799	29-Oct	29-Oct	7
1977	863	24-Oct	25-Oct	7
1978	414	30-Oct	30-Oct	8
1979	1104	29-Oct	30-Oct	8
1980	809	31-Oct	1-Nov	8
1981	1418	26-Oct	26-Oct	9
1982	797	25-Oct	25-Oct	8
1983	427	28-Oct	27-Oct	10
1984	318	24-Oct	25-Oct	9
1985	238	23-Oct	25-Oct	9
1986	249	27-Oct	27-Oct	8
1987	260	30-Oct	30-Oct	9
1988	133	28-Oct	27-Oct	9
1989	83	25-Oct	25-Oct	7
1990	42	22-Oct	23-Oct	7
1991	82	25-Oct	28-Oct	8
1992	113	21-Oct	22-Oct	8
1993	95	22-Oct	23-Oct	7
1994	98	27-Oct	25-Oct	7
1995	209	27-Oct	28-Oct	10
1996	339	25-Oct	24-Oct	7
1997	386	20-Oct	22-Oct	8
1998	453	28-Oct	29-Oct	11
1999	677	27-Oct	27-Oct	10
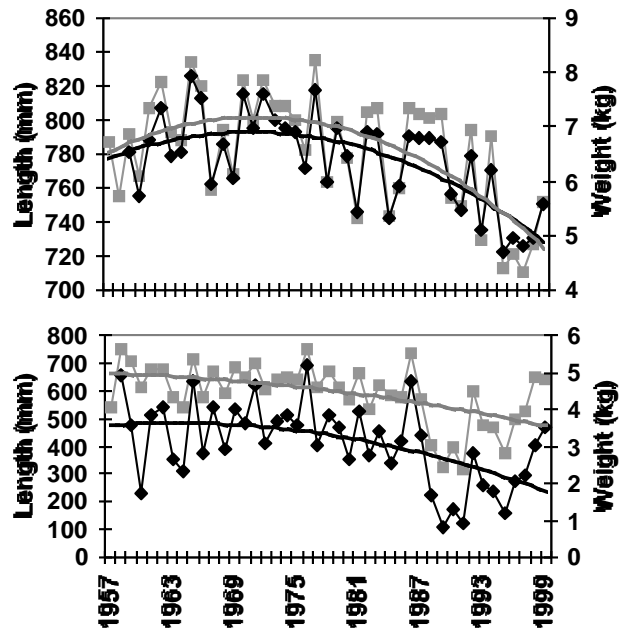
Figure 10. *Mean lengths and weights of male and female chinook salmon (all ages combined) over time(1957-1999).*

females and males ages 1 and 3+. Females have been declining in size gradually over the last 40+ years. The male chinook sometimes with extreme year to year variation have been declining in size over time at age-1, while the age-2 males have had no significant change over time except the drastic drop from 1986 through 1992, and the age-3+ males tended to become larger until 1990 when their size started to decrease (Figure 11). As with the coho salmon, the chinook salmon have shown lower condition factor in the 1980's and 1990's compared to the early years (1950's-1970's). However, the chinook did not see the drastic decline in condition until the late 1980's (~1988), whereas the coho experienced the decline starting in 1980 (Figure 12).

Fecundity and egg size

The chinook female lengths were adjusted to a standard length [overall mean of all female lengths] of 785 mm for weight, fecundity, and egg size. The adjusted fecundity increased from the late 1950's to the end of the
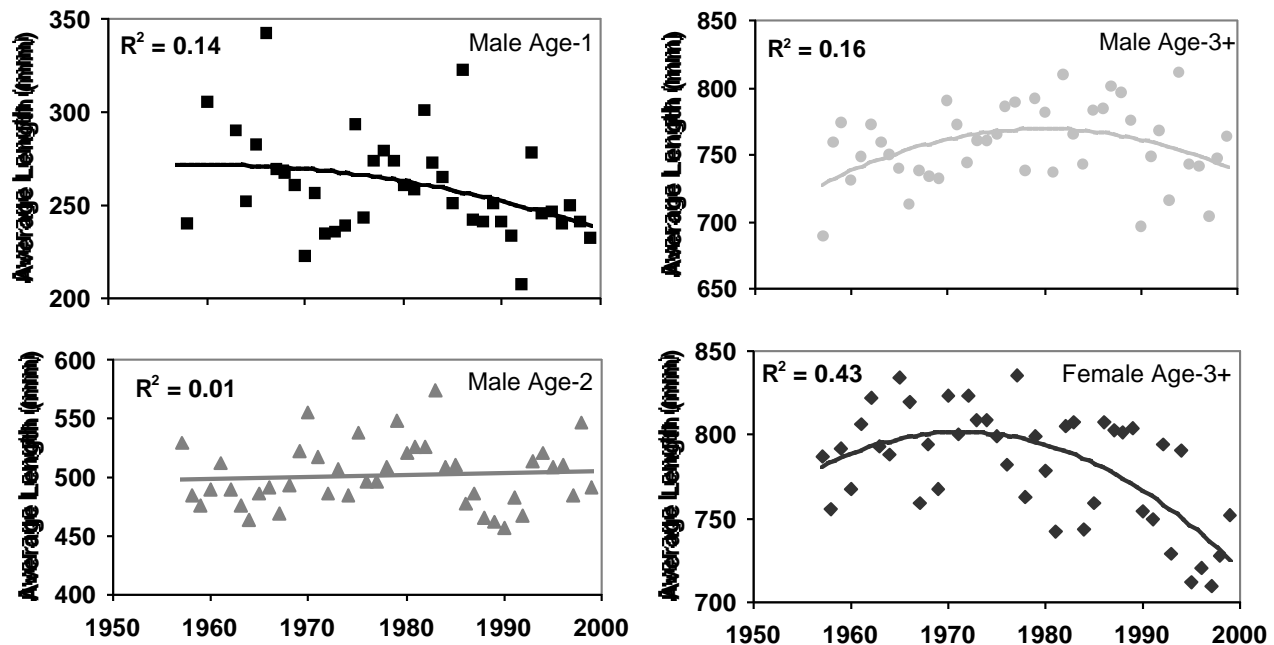
Figure 11. *Average length at age of male and female chinook salmon indicating change in length over the period of time from 1957-1999 of the UW population.*
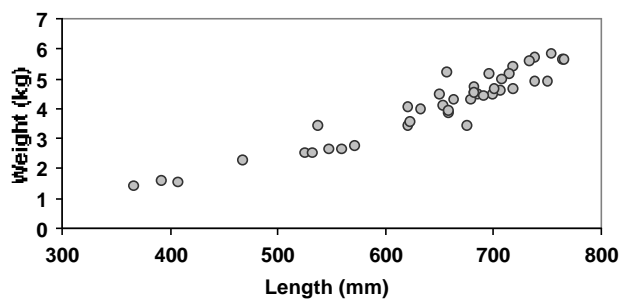

Figure 12. *Condition factor (allometric relationship) of all male and female chinook salmon. Each circle represents an individual year that ranges from 1957-1999.*

1970's, but since the early 1980s it has declined (Figure 13). Egg size, adjusted to the standard length, showed no change in size over time but the variability of egg size among years was very high and it tended to vary inversely with fecundity.

Precocious Maturity

UW chinook salmon show two age groups of mature males not seen in females: ages 1 (mini-jacks) and 2 (jacks). The jacks have been recorded since the hatchery's beginning in relatively high numbers, whereas

the mini-jacks were first recorded in 1956, when 52 returned. As the proportion of mini-jacks has increased, the number of 2-year old jacks has decreased (Figure 14). The proportion of jacks returning to the total male returns shows a similar trend of 2-year old jacks decreasing in proportion as the 1-year old jacks increase in proportion over time (Figure 15).

Discussion

Spawning Date

Pacific salmon return to their natal streams to spawn, which results in the segregation of spawning adults in time and location (Murray et al. 1990). Pacific salmon also seem to be genetically adapted to specific spawning times, locations, and temperatures (Murray et al. 1990) and indirectly to specific incubation temperatures. Our results indicated that both the coho and chinook time of spawning is earlier than in the past. Coho salmon generally spawn later and at lower temperatures than chinook salmon but have a higher develop-
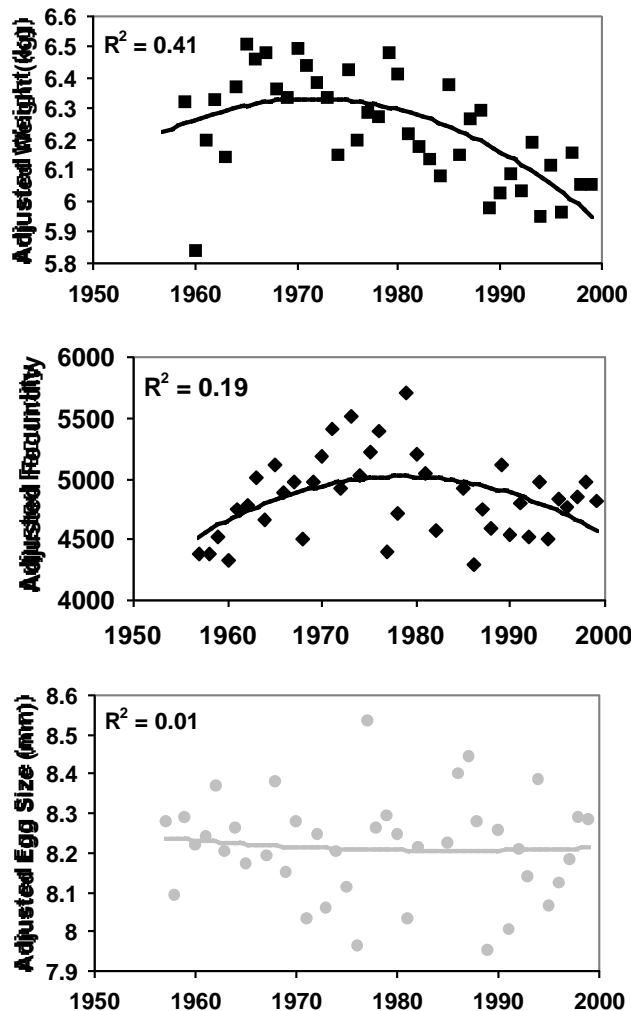
Figure 13. *Female chinook weight (graph1), fecundity (graph 2), and egg size (graph 3) adjusted to a standardized length of 785mm from 1957-1999.*

Figure 14. *The number of mini-jacks (age-1) and jacks (age-2) that returned to the UW hatchery from 1957-1999.*

Figure 15. *The proportion of mini-jack (age-1) and jack (age-2) returns to the total number of male returns that entered the UW hatchery ponds from 1957-1999.*

mental rate and emerge sooner than other Pacific salmon at all temperatures (Murray and McPhail 1988; Murray et al. 1990). This developmental rate may be a mechanism for synchronizing fry emergence with other salmon species in the spring (Murray and McPhail 1988; Murray et al. 1990). It is common for hatchery practices to result in earlier spawning timing (Flagg et al. 1995).

Early arriving salmon are spawned at the hatchery and in some years late fish were surplus to the capacity of the facility and so they were not spawned. Moreover, offsprin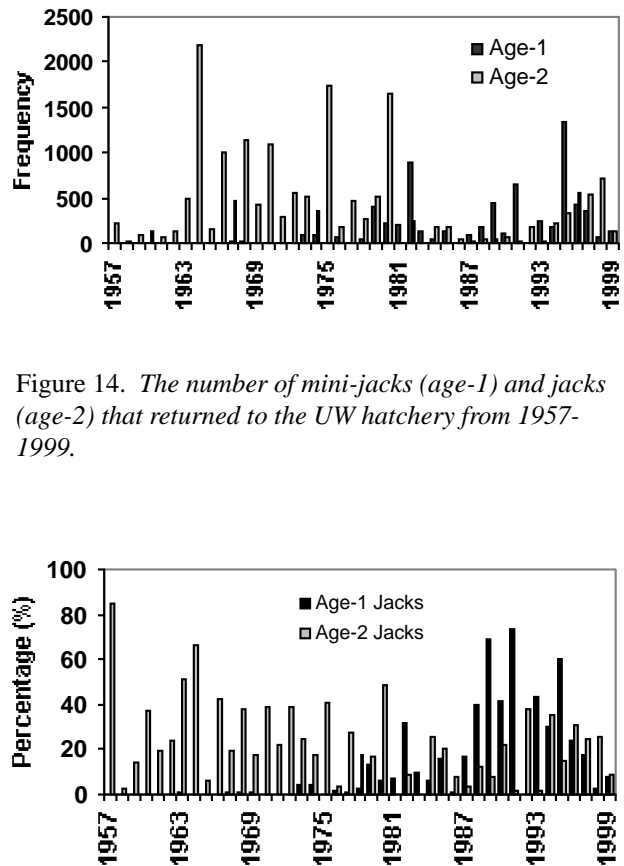g of late-spawning parents would begin feeding later in the spring than the offspring of earlier spawners, and so have a marked size disadvantage during common rearing and perhaps not reach a suitable size for smolt transformation and seawater entry. This is particularly important for the coho salmon, which must reach smolt size by the end of their first spring. It is very unlikely that the offspring of females spawning in January and February would grow and survive at comparable rates to earlier spawners, given this constraint.

Change in body size

The decline in body size by length and weight, and condition factor over time was evident in the University of Washington coho

and chinook hatchery salmon populations. The decline in body size has been shown in other studies throughout the Pacific northwestern United States, including Alaska, and British Columbia (Helle and Hoffman 1995, 1998; Pyper and Peterman 1999). Recent evidence suggests that competition for food and ocean conditions (e.g., sea-surface temperatures) may contribute to temporal variation in adult body size (McKinnell 1995; Pyper and Peterman 1999). Pyper and Peterman (1999) indicated that increases in total sockeye abundance and sea-surface temperatures were major factors in the reduction of adult body length, and they concluded that abundance appeared to have a greater effect on body length than temperature. Increased production levels of salmon at hatcheries, including the University of Washington, may explain some of the decline in size. However, the sockeye salmon are much more abundant than the coho and chinook salmon so the extent of density-dependence is unclear. Alternatively, the rearing in the hatchery environment with increased temperatures and better, more nutritious food in large quantities may be contributing to the decline in adult size. To the extent that large smolts are more likely to mature at earlier ages than smaller ones, any trends in smolt size may be reflected in adult size as well. Examination of smolt size data is planned to test this effect.

Fecundity and egg size

The adjusted fecundities of both the coho and chinook populations increased in the early years (up through the 70's) but since that time have been declining. The decline in chinook fecundity, like other salmon populations, is a function of decreased fish body size because of the decrease in available space for the eggs. Chinook salmon adjusted egg size showed no change over time, although variation among years was high. Coho salmon adjusted fecundities have shown an inverse

relationship with adjusted egg diameter; when the fecundity declined the egg size increased and when the egg size decreased fecundity increased. This trend may be explained by the fact that rapid growth is associated with a high fecundity for a given length (e.g., Jonsson et al. 1996). Egg size is also affected because salmon adjust egg size to accommodate egg number, given the energetic constraints of gonad production. UW coho and, to a lesser extend chinook, are expressing the results of poor feeding conditions with fewer but larger eggs for a given body length.

Precocious Maturity

Many salmon species include males that mature earlier, thus returning at a much smaller size compared to other adult body sizes of males in the population (Gross 1985). Accelerated incubation and rearing of coho can result in the production of precocious spawners or age-1 jacks, returning after only 5 to 6 months of marine residence, initiated by higher incubation temperatures and facilitated with a large amount of nutritious food (Brannon et al. 1982). The chinook were also reared under these conditions and exhibit the same response of early maturity and return of jacks aged one and two, due to the higher incubation temperatures and increased growth rates continued with the large amounts of good quality food. This hypothesized relationship between smolt size and proportion of jacks will be tested in the future with the available data. It is interesting that the proportion of age-1 coho and chinook jacks increased during the periods when length, weight and fish condition factor were declining. In any case, the increasing number of jacks does not result from but rather it runs counter to genetic selection, as jacks are not used for spawning. Therefore, the accelerated incubation and growth at the hatchery seems to be the best explanation for the high number of returns of jacks for coho and chinook populations.

Acknowledgements

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